Seedbank and Emerged Weed Communities Following Adoption of Glyphosate-Resistant Crops in a Long-Term Tillage and Rotation Study

Lynn M. Sosnoskie, Catherine P. Herms, John Cardina, and Theodore M. Webster*

The compositions of the germinable weed seedbank and aboveground weed communities in a long-term tillage and rotation study were characterized 4, 5, and 6 yr (2002 to 2004) after the adoption of glyphosate-tolerant corn and soybean. Averaged across rotation, mean germinable weed seed density and diversity were greatest in the no-tillage treatment as compared to the minimum- and conventional-tillage treatments. Averaged over tillage, density and diversity were greater in the corn-oat-hay (ryegrass + alfalfa) system as compared to the continuous corn and corn-soybean rotations. Similar trends in density and diversity were observed for the aboveground weed communities. Differences in community composition among treatments were quantified with the use of a multiresponse permutation procedure. Results indicated that the weed seedbank community in a corn-oat-hay rotational system differed from the communities associated with the continuous corn and corn–soybean rotational systems. Weed seedbank communities developing under a no-tillage operation differed from those in minimum- and conventional-tillage scenarios. Compositional differences among the aboveground weed communities were less pronounced in response to tillage and rotation. Indicator species analyses indicated that the number of significant indicator weed species was generally higher for no tillage than minimum or conventional tillage for both the seedbank and the aboveground weed communities. The number of significant indicator species for the seedbank and weed communities was generally greater in the three-crop rotation as compared to the continuous corn and corn-soybean rotations. The trends observed in density, diversity, and community composition after the adoption of glyphosate-tolerant corn and soybeans, and a glyphosate-dominated weed management program, were also observed when soil-applied herbicides were included in the study. We suggest that the switch to a POST-glyphosate protocol did not significantly alter weed communities in the short term in this study.

Nomenclature: Glyphosate; alfalfa, Medicago sativa L.; corn, Zea mays L.; oat, Avena sativa L.; ryegrass, Lolium perenne L.; soybean, Glycine max (L.) Merr.

Key words: Weed communities, tillage, rotation, glyphosate, indicator species.

The abundance and composition of species in arable weed seedbanks and aboveground weed communities reflect past and current management of soils, crops, and weeds (Anderson et al. 1998; Bàrberi et al. 1998; Cavers and Benoit 1989; Feldman et al. 1997; Légerè and Samson 1999; Menalled et al. 2001; Tørresen and Skuterud 2002). Weed species density and diversity are affected by tillage (Anderson et al. 1998; Tuesca et al. 2001), crop rotation (Cardina et al. 2002; Davis et al. 2005), crop and weed management (Bàrberi et al. 1998; Menalled et al. 2001), and local environmental conditions. The principal species flourishing under intense tillage can differ from those dominating systems with little or no soil disturbance (Anderson et al. 1998; Bàrberi et al. 1998; Bàrberi and Lo Cascio 2001; Feldman et al. 1997; Tørresen and Skuterud 2002). Crop rotation has been shown to influence the composition of weed communities, mostly because of the effects of weed management in sequential crops. There is also evidence to suggest that crop rotation, independent of herbicides, is important in altering weed communities (Liebman and Dyck 1993). Several mechanisms could be responsible for this effect, including allelopathy, microbial community changes, and differential resource partitioning, which could influence seed production or survival of seeds in the seedbank. Differences in crop height, density, and canopy architecture can also favor some weed species over others (Leroux et al. 1996).

The commercial release and widespread adoption of genetically modified glyphosate-tolerant crops (GTCs) has

transformed a significant proportion of the agricultural landscape (Duke 2005). In 2004, 80, 60, and 73% of the soybean, cotton (Gossypium hirsutum L.), and canola (Brassica napus L.) hectarage in the United States were glyphosate tolerant (Duke 2005). Despite the potential benefits of GTCs, such as flexible timing of control, improved weed control, reduced tillage, and easier harvest (Freyssinet 2003; Kuiper et al. 2000; Riches and Valverde 2002), there is concern that the widespread use of a single herbicide mode of action across space and time will alter agricultural weed community dynamics in crop fields (through species shifts and the development of herbicide-resistant weeds), which could have serious economic and ecological ramifications (Blackburn and Boutin, 2003; Culpepper et al. 2006; Freyssinet 2003; Kuiper et al. 2000; Lyon et al. 2002; Martinez-Ghersa et al. 2003; Powles and Shaner 2001; Riches and Valverde 2002; Zoschke 1994).

Previously published research has described the seed depth distribution and abundance and diversity of individual weed species in an experiment where three tillage systems and three crop sequences have been in place since 1962 (Cardina et al. 2002; Sosnoskie et al. 2006). After soil-applied and postemergence herbicides were used for 35 yr, glyphosate-tolerant corn and soybean varieties were introduced into the study and the seedbank and aboveground components of the weed communities, with respect to density, diversity, and composition, were characterized. Additionally, indicator species analysis were used to identify species that might serve as a measure of the environmental conditions resulting from particular combinations of tillage system and crop rotation.

Materials and Methods

The study was conducted in a long-term tillage and rotation experiment initiated in 1962 (Triplett-Van Doren

DOI: 10.1614/WS-08-147.1

^{*} First, second, and third authors, Department of Horticulture and Crop Science, The Ohio State University, Wooster, OH 44691; fourth author, Crop Protection and Management Research Unit, USDA-ARS, Tifton, GA 31794. Current address of first author: Department of Crop and Soil Sciences, University of Georgia, 4604 Research Way, Tifton, GA 31794. Corresponding author's Email: cardina.2@osu.edu

No-Tillage Experimental Plots) at Wooster, OH. Climate, soil, and site characteristics, as well as details of the experimental design, have been described previously (Cardina et al. 2002; Dick and Van Doren 1985; Sosnoskie et al. 2006). The experiment is a factorial arrangement of three tillage systems and three crop-rotation treatments replicated three times in a randomized complete block design. The three tillage systems were no tillage (NT), minimum tillage (MT), and conventional tillage (CT). The CT plots were moldboard plowed to a depth of 20 to 25 cm, followed by two disking operations before planting; the MT plots were chisel plowed and disked once before planting. The NT plots did not receive any mechanical disturbance except for the passage of the coulter unit. The three rotation systems were continuous corn (CC), corn–soybean, and corn–oat–hay (alfalfa plus ryegrass). In order to avoid confounding with weather conditions, each crop of each rotation appeared every year (Cardina et al. 2002; Sosnoskie et al. 2006). Therefore, there are separate plots for corn followed by (fb) soybean (CS) as well as soybean fb corn (SC). Likewise, for the three-crop rotation, there are separate plots for corn fb oat fb hay (COH), oat fb hay fb corn (OHC), and hav fb corn fb oat (HCO). This resulted in a total of six rotation and three tillage treatments with three replications, for a total of 54 plots. Individual plots are 5 m wide and 21 m long.

Glyphosate-tolerant corn ('Dekalb DKC58-53RR') was planted at a rate of 87,851 seeds ha⁻¹ in rows 76 cm apart; glyphosate-tolerant soybean ('Pioneer 93B36RR') was drilled at a rate of 77 kg ha⁻¹ in rows 18 cm apart. Corn and soybeans were seeded April 28, 2002, May 23, 2003, and April 30, 2004, with the delay in 2003 due to wet soil conditions. Oat (77 kg ha⁻¹ 'Armor'), alfalfa (13 kg ha⁻¹ 'Croplan Rocket') and ryegrass (7 kg ha⁻¹) were seeded with a no-tillage drill. Fertilizer and lime were applied following Ohio State University soil test recommendations, and the same rates of N, P, and K were used in each tillage system.

All NT plots received a single, early-spring application of glyphosate (1.12 kg ae ha⁻¹) prior to planting, except in 2004, when this application occurred 20 d after planting (DAP). All corn and soybean plots received a POST application of glyphosate (1.12 kg ha⁻¹) between 4 and 8 wk after planting (WAP). Except for 2004, bromoxynil (0.42 kg ai ha⁻¹) was applied during the first week in May to control broadleaf weeds in oat plots. No herbicides were applied to the hay crops except for glyphosate to kill existing vegetation prior to planting.

Sample and Data Collection. To characterize the seedbank, soil samples were collected in March each year. Twelve samples, consisting of two soil cores each, were obtained from each plot. Each soil core was 3.5 cm in diameter and 5 cm deep. The samples were evenly distributed in the plots (a minimum 1-m distance between samples, and a minimum 1.5-m distance from plot borders). Samples were processed by sieving through a 0.64-cm screen. An entire sample (two cores), minus large stones and root fragments, was spread over a 2.5-cm layer of ProMix BX¹ potting media (to improve drainage) in a 15-cm² tray and placed on a mist bench. Emerged weed seedlings were identified, counted, and removed weekly. Taxa that were difficult to identify to the species level at the seedling stage were classified as a single species (i.e., *Digitaria* spp., *Setaria* spp.). The positions of the

trays were rerandomized regularly. After emergence ceased (about 4 mo), samples were placed in a 4 C cold room for 8 wk to break secondary dormancy in the remaining seeds. Soil samples were stirred and resieved before being returned to the greenhouse (Cardina and Sparrow 1996)

To characterize the aboveground component of the weed community, emerged weeds were counted in June, prior to the POST application of glyphosate in corn and soybeans. All annual weeds in four 0.25-m² sampling quadrats per plot were identified and counted. For perennial species, the number of aboveground shoots occurring in each 0.25-m² quadrat was counted. The sampling areas were spaced at regular intervals (approximately 3 m apart) within each plot, and were at least 1.5 m from the plot borders.

Data Analysis

The germinable seed and aboveground weed density data were converted to the number of seeds m⁻² and weeds m⁻², respectively. Species richness, the number of weed species per plot, was also calculated from the density data. When necessary, the density and richness values were transformed prior to analysis to improve normality and homogeneity of variance. Seed and weed density and species richness data were compared across the three tillage systems (NT, MT, and CT) and six cropping sequences (CC, CS, SC, COH, OHC, HCO) with the use of Proc Mixed in SAS.² The interaction between tillage and rotation was also evaluated. Replication and the interactions between replication and the main effects were considered as random factors. Differences in weed seed and in-field weed community composition were evaluated with the use of the multiresponse permutation procedure (MRPP) in PC-ORD³ in accordance with the recommendations of McCune and Grace (2002). The multivariate MRPP analysis tests the null hypothesis that two or more a priori defined groups are not different with respect to composition (Biondini et al. 1988; Zimmerman et al. 1985), and provides a test statistic with an associated probability value (McCune and Grace 2002). For both types of analyses (Proc Mixed and MRPP), years were analyzed separately.

Indicator species analysis was used to describe the association of individual weed species with each of the tillage and rotation treatments with the use of a protocol established by Dufrêne and Legendre (1997). Indicator values (IV $_{jk}$) were calculated as

$$IV_{jk} = 100 \times A_{jk} \times F_{jk}, \qquad [1]$$

where A_{jk} and F_{jk} are the relative abundance and the relative frequency, respectively, of species j in treatment k (Dufrêne and Legendre 1997; McCune and Grace 2002). Indicator values can range from zero (no association with a treatment) to 100 (absolute association with a treatment). The statistical significance of the maximum indicator value for each species within each treatment class (tillage and rotation) was evaluated with the use of a Monte Carlo test with 1,000 iterations in PC-ORD. Years were analyzed separately.

Results and Discussion

We identified 46, 47, and 37 weed species in the 2002, 2003, and 2004 seedbanks, respectively (Table 1). A total of

Table 1. Frequency of occurrence (percent of plots) of individual weed species in the springtime seedbank and summertime weed communities for 2002, 2003, and 2004.

			Seedbank			Field	Field	
Common name	Scientific name	2002	2003	2004	2002	2003	2004	
Velvetleaf	Abutilon theophrasti Medicus	0	0	0	2	6	7	
Virginia copperleaf	Acalypha virginica L.	15	0	0	4	2	4	
Redroot pigweed	Amaranthus retroflexus L.	80	61	69	65	70	80	
Other pigweeds	Amaranthus spp.	11	0	0	0	0	0	
Common ragweed	Ambrosia artemisiifolia L.	4	2	0	7	2	4	
Scarlet pimpernel	Anagallis arvensis L.	0	0	0	0	2	0	
Mayweed chamomile	Anthemis arvensis L.	0	0	0	0	4	0	
Hemp dogbane	Apocynum cannabinum L.	0	0	0	0	2	0	
Common burdock	Arctium minus (Hill) Bernh.	0	0	0	0	0	2	
Nodding beggarticks	Bidens cernua L.	15	0	0	0	0	0	
Mustards	Brassica spp.	24	0	0	0	0	0	
Bromes	Bromus spp.	0	0	0	4	0	0	
Shepherd's-purse	Capsella bursa-pastoris (L.) Medicus	46	54	15	17	33	17	
Hairy bittercress	Cardamine hirsuta L.	59	67	61	24	50	48	
Mouseear chickweed	Cerastium vulgatum L.	0	0	0	0	0	11	
Common lambsquarters	Chenopodium album L.	91	96	80	72	74	67	
Canada thistle	Cirsium arvense (L.) Scop.	4	0	0	20	4	6	
Horseweed	Conyza canadensis (L.) Cronq.	7	7	9	6	0	2	
Yellow nutsedge	Cyperus esculentus L.	67	2	2	9	7	11	
Jimsonweed	Datura stramonium L.	0	0	0	0	2	0	
Wild carrot	Daucus carota L.	0	0	2	2	0	0	
Crabgrasses	Digitaria spp.	69	59	87	74	63	78	
Barnyardgrass	Echinochloa crus-galli (L.) Beauv.	0	2	17	4	19	20	
Quackgrass	Elymus repens (L.) Gould	0	0	0	7	0	0	
Field horsetail	Equisetum arvense L.	0	2	0	Ó	0	0	
Annual fleabane	Erigeron annuus (L.) Pers.	26	43	22	9	4	31	
boneset	Eupatorium perfoliatum L.	48	0	0	0	0	0	
Spotted spurge	Chamaesyce maculata (L.) Small	7	26	9	15	2	11	
Fescues	Festuca spp.	0	0	0	13	9	4	
Hairy galinsoga	Galinsoga quadriradiata Cav.	0	11	0	0	0	0	
Geranium		0	0	2	2	2	2	
	Geranium spp.	2	2	0	2	0	2	
Ground ivy	Gleochoma hederacea L.	9	17		0	2	0	
St. Johnsworts	Hypericum spp.	0	0	11 0	0	0		
Jewelweed	Impatiens capensis Meerb.						2	
Rushes	Juncus spp.	57	76	28	4	2	2	
Prickly lettuce	Lactuca serriola L.	0	0	0	0	2	4	
Purple deadnettle	Lamium purpureum L.	35	15	54	4	15	22	
Field pepperweed	Lepidium campestre (L.) R.Br.	0	0	0	0	2	0	
Indiantobacco	Lobelia inflata L.	41	67	39	6	20	22	
Common mallow	Malva neglecta Wallr.	0	2	0	2	7	0	
Carpetweed	Mollugo verticillata L.	6	6	11	6	0	0	
Wirestem muhly	Muhlenbergia frondosa (Poir.) Fern.	9	0	7	2	0	6	
Nimblewill	Muhlenbergia schreberi J.F.Gmel.	4	7	0	0	2	0	
Yellow woodsorrel	Oxalis stricta L.	94	78	74	52	59	48	
Witchgrass	Panicum capillare L.	52	59	70	44	50	41	
Fall panicum	Panicum dichotomiflorum Michx.	70	56	78	54	76	74	
Common pokeweed	Phytolacca americana L.	0	4	0	6	4	13	
Broadleaf plantain	Plantago major L.	54	65	57	37	28	44	
Annual bluegrass	Poa annua L.	30	37	35	32	59	56	
Prostrate knotweed	Polygonum aviculare L.	4	9	2	7	7	15	
Wild buckwheat	Polygonum convolvulus L.	0	2	4	7	7	15	
Pennsylvania smartweed	Polygonum pensylvanicum L.	69	15	19	20	26	44	
Common purslane	Portulaca oleracea L.	30	33	57	39	35	22	
Oldfield cinquefoil	Potentilla simplex Michx.	54	2	2	0	0	0	
Yellowcress	Rorippa spp. 1	9	0	0	0	0	0	
Docks	Rumex spp.	13	6	2	9	4	7	
Common groundsel	Senecio vulgaris L.	0	0	7	26	26	19	
Foxtails	Setaria spp.	80	28	52	52	67	61	
Eastern black nightshade	Solanum ptycanthum Dun.	46	15	39	28	26	28	
Nightshades	Solanum spp.	7	0	0	0	0	0	
Goldenrods	Solidago spp.	4	17	6	2	0	0	
Sowthistles	Sonchus spp.	22	22	20	26	22	15	
Common chickweed	Stellaria media (L.) Vill.	32	50	15	39	70	65	
Dandelion	Taraxacum officinale Weber in Wiggers	41	56	41	96	91	98	
		0	13	6	96 6		98 7	
Field pennycress	Thlaspi arvense L.					13		
Unknown tree	Trifolium onn	0	6	0	4	19 25	17	
Clovers	Trifolium spp.	6	9.3	0	12	35	13	
Common venuslookingglass	Triodanis perfoliata (L.) Nieuwl. Var. perfoliata	0	12	0	0	0	0	
Cattails	Typha spp.	2	6	4	0	0	0	
Stinging nettle	Urtica dioica L.	4	2	0	0	0	0	
Common mullein	Verbascum thapsus L.	0	2	0	0	0	0	
Speedwells	Veronica spp.	78	87	76	33	87	52	

Table 2. Mean weed seed density and species richness in response to tillage and rotation for 2002, 2003, and 2004.

Treatment		Weed seed density	Weed seed species richness				
	2002	2003	2004	2002	2003	2004	
		No. m ⁻²	No. per plot				
Tillage							
$\operatorname{CT}^{\operatorname{a}}$	2,510 c ^b	2,370 c	3,380	15	12	9 Ь	
MT	3,770 b	6,220 b	5,670	16	14	13 a	
NT	5,540 a	8,390 a	7,750	16	15	13 a	
Rotation							
CC^{c}	2,390 с	4,740 cd	3,600 b	14 b	11 de	10 c	
CS	1,580 c	2,290 d	2,970 b	14 b	10 e	11 bc	
SC	1,780 c	4,980 bc	2,070 b	14 b	13 cd	10 c	
COH	8,790 a	7,810 a	8,650 a	17 a	16 ab	13 ab	
OHC	3,880 Ь	8,660 a	7,680 a	16 ab	18 a	15 a	
HCO	5,230 b	5,370 ab	10,470 a	18 a	14 bc	13 a	

^a CT, conventional tillage; MT, minimum tillage; NT, no tillage.

20,140 seedlings were identified during the course of the study. Redroot pigweed (Amaranthus retroflexus L.), hairy bittercress (Cardamine hirsute L.), crabgrasses (Digitaria spp.), common lambsquarters (Chenopodium album L.), yellow woodsorrel (Oxalis stricta L.), witchgrass (Panicum capillare L.), fall panicum (Panicum dichotomiflorum Michx.), and speedwells (Veronica spp.) were the most commonly encountered species, occurring in over 60% of the plots. Many of the same species were also abundant in prior seedbank studies conducted in the Triplett-Van Doren No-Tillage Experimental Plots (Cardina et al. 2002; Sosnoskie et al. 2006). In the emerged weed surveys, 48, 48, and 45 species were documented in 2002, 2003, and 2004, respectively (Table 1). A total of 31,950 seedlings were identified in the field over the 3 yr of the study. Averaged over years, the most frequently encountered species was dandelion (Taraxacum officinale Weber in Wiggers), which occurred in over 95% of the field plots. The next most common species were redroot pigweed in 72% of plots, crabgrasses (72%), common lambsquarters (71%), fall panicum (68%), and yellow woodsorrel (60%). A total of 72 species were identified in the germinable seedbank and in-field weed emergence studies from 2002 through 2004. There were 46 species common to both seedbank and emerged weed surveys; approximately 57% of these common species were present in both surveys all 3 yr. In general, the most abundant species in the seedbanks were also the most frequently encountered species in the emerged weed surveys.

Weed Seedbank Density. Mixed-model ANOVA indicated that the numbers of germinable weed seeds, to a depth of 5 cm, in the 2002 and 2003 springtime seedbanks were influenced by tillage ($P \le 0.05$; Table 2). For both years, mean seed density increased as soil disturbance decreased (NT > MT > CT). Although the differences in seed densities among tillage treatments were not significant in 2004, the same tendency toward higher seed numbers in NT, as compared to CT and MT, was observed. Averaged over years and crop rotations, NT plots had the highest seed density (7,230 seeds m⁻²), followed by MT (5,220 seeds m⁻²), and CT (2,750 seeds m⁻²). These results agree with observations made by Bàrberi and Lo Cascio (2001), Cardina et al. (2002), Menalled et al. (2001), Tørresen and Skuterud (2002), and Tørresen et al. (2003), and suggest that seeds

accumulate closer to the soil surface when tillage intensity is minimized. Sosnoskie et al. (2006) observed a similar trend in weed seed density in the same research plots prior to the inclusion of GTCs. Crop rotation also had a significant effect on weed seed density all 3 yr ($P \le 0.05$; Table 2). Except for the HCO treatment in 2003, mean weed seed numbers m⁻² were greater in the three-crop rotation treatments than in the CC, CS, and SC treatments. Averaged over tillage systems and years, mean seed densities in COH, OHC, and HCO ranged from 3,880 to 10,470 seeds m⁻², whereas seed densities in the one- and two-crop rotations ranged from 1,580 to 4,980 seeds m⁻². Analyses of variance indicated that there were no interactions between the main effects of tillage and rotation for seed density in 2002 and 2003. An interaction was detected in 2004, although there were no patterns in the observed seed densities that could be directly attributed to the treatments (data not shown).

Weed Seedbank Diversity. Species richness of the germinable weed seedbank was significantly (P \leq 0.05) influenced by tillage in 2004 (Table 2). Weed seed diversity in 2004 was higher in NT (13 species) and MT (13 species) than in the CT (9 species). Although not significant, there was a trend toward greater numbers of weed species in the seedbanks of NT and MT as compared to CT in 2002 and 2003. These results agree with those of Carter and Ivany (2006), Feldman et al. (1997), and Sosnoskie et al. (2006), who also reported that species diversity was higher when tillage intensity was reduced. Crop rotation also influenced weed seed species richness all 3 yr (P \leq 0.05; Table 2). With few exceptions, species richness was greater in the COH, OHC, and HCO (13 to 18 species per plot) than in the CC, CS, and SC rotations (10 to 14 species). Greater variability in crop production practices should diversify the selection pressures acting on an agricultural system and result in communities that are less dominated by one or a few species or functional groups (Anderson et al. 1998). It has been suggested that increased weed species diversity is beneficial to an agroecosystem if the resident species are providing some benefits, such as facilitating nutrient cycling or supporting faunal diversity (Feldman and Boyle 1998; Sturz et al. 2001; Swift and Anderson 1993). However, the benefits of increased diversity would be diminished if the resultant species were significant

^b Means within a column and treatment followed by the same letter are not different at the $\alpha = 0.05$ level. The absence of letters indicates that the F values for the main effects of tillage and rotation were not significant at the $\alpha = 0.05$ level.

^c CC, continuous corn; CS, corn fb soybean; SC, soybean fb corn; COH, corn fb oat fb hay; OHC, oat fb hay fb corn; HCO, hay fb corn fb oat.

Table 3. Mean emergent weed density and species richness in response to tillage and rotation for 2002, 2003, and 2004.

Treatment	E	merged weed densit	y	Emerged weed species richness				
	2002	2003	2004	2002	2003	2004		
	<u></u>	No. m ⁻²				plot		
Tillage								
CT^a	100 b ^b	210	100 b	9	13	12 b		
MT	190 b	290	170 a	9	13	14 a		
NT	360 a	330	90 b	12	14	11 b		
Rotation								
CC^{c}	180 b	350 ab	100 b	10 b	12 b	10 c		
CS	170 b	230 bc	110 b	12 b	13 b	10 c		
SC	160 bc	250 bc	50 c	10 b	12 b	8 d		
COH	610 a	420 a	90 b	15 a	19 a	11 c		
OHC	100 cd	180 c	200 a	7 c	12 b	19 a		
HCO	80 d	220 bc	170 ab	7 c	12 b	15 b		

^a CT, conventional tillage; MT, minimum tillage; NT, no tillage.

competitors that reduced the quantity and quality of crop yield (Légère et al. 2005). Davis et al. (2005) reported a negative relationship between weed diversity and crop yield.

Emerged Weed Density. Aboveground weed densities in 2002 and 2004 were affected by tillage (P \leq 0.05; Table 3). In 2002, mean weed density increased as soil disturbance decreased (NT > MT \geq CT; Table 2). In 2004, mean weed density was almost two times higher in the MT (170 plants m⁻²) treatment than in the NT (90 plants m⁻²) and CT (100 plants m⁻²) treatments. Except in 2004, when a single glyphosate treatment was made 20 DAP in both corn and soybeans, all NT plots received an early-spring preplant application of glyphosate. The delayed burn down application in 2004 occurred just prior to the field survey and likely accounted for the lower weed numbers observed in the NT system when averaged over rotation. Although the differences in aboveground densities among tillage treatments were not significant in 2003, there was a tendency toward increased mean weed density in treatments where tillage intensity was reduced (NT and MT).

Crop rotation significantly (P ≤ 0.05) affected aboveground weed densities all 3 yr (Table 3). The highest densities occurred in the COH plots in 2002 (610 plants m⁻²) and $2003 (420 \text{ plants m}^{-2})$, and the OHC ($200 \text{ plants m}^{-2}$) and HCO (170 plants m⁻²) plots in 2004. Patterns in emerged weed densities reflect weed management practices employed in both the current and previous years' crops. For example, in 2002 and 2003, emerged weed densities were lower in the OHC treatment because oats received an application of bromoxynil for control of broadleaf weed species just prior to the field counts. In 2002, the hay crop was replanted in late spring, so spring and summer weeds were killed just prior to the survey. Greater weed densities in the COH treatment in 2002 and 2003 may be due to the absence of chemical weed management efforts in the preceding hay crop. There was a significant (P \leq 0.05) interaction between tillage and rotation for aboveground weed density in 2004. Greater weed numbers were observed in MT-OHC (260 plants m⁻²) and MT-HCO (330 plants m⁻²) treatments as compared to the others (30 to 190 plants m⁻²) and were likely the result of the combined effects of the missed bromoxynil and late glyphosate (20 DAP) applications in the oat and NT-corn and NT-soybean plots, respectively (data not shown).

Emerged Weed Diversity. Weed species richness was significantly (P \leq 0.05) influenced by tillage in 2004. Species richness was greater in the MT (14 species per plot) system as compared to the CT (12 species) and NT (11 species) systems (Table 2). Although the differences among treatments were not significant, there was a trend toward greater numbers of weed species in the NT and MT treatments as compared to the CT treatment for the emerged weed communities in 2002 and 2003. Crop rotation also influenced species richness $(P \le 0.05; Table 3)$. Except for 2004, when an average of 19 species had emerged in the OHC plots, values for species richness were greatest in COH plots, with 15 species in 2002 and 19 in 2003. The trends in weed species diversity among treatments mirrored the trends observed in weed density. As with weed density, species richness in the OHC treatments was lower in 2002 and 2003 studies because of the timing of the bromoxynil applications; greater species richness in the 2002 and 2003 COH treatments in 2002 and 2003 was likely due to the absence of chemical weed management efforts in the preceding hay crop. There was a significant (P ≤ 0.05) interaction between tillage and rotation for species richness in 2004. Weed species richness was higher in the MT-OHC (22 species), MT-HCO (19 species) and NT-OHC (20 species) treatments relative to the others (6 to 16 species) (data not shown).

Community Composition. Results from MRPP analyses indicated that the composition of the germinable springtime weed seedbank was influenced by tillage and rotation (Table 4). The weed seed community in the NT plots differed from the community present in the CT plots all 3 yr $(P \le 0.015)$. The CT vs. MT and MT vs. NT comparisons were significant only in 2003. These results suggest distinct trajectories for weed communities where soil disturbance is minimized (NT) as compared to plots where the soil and plant residue are highly disturbed by plowing (CT). The weed seedbank communities in the three-crop rotation differed from those in the CC, CS, and SC rotations in 25 of 27 comparisons (P \leq 0.003). Results from MRPP analyses also

^b Means within a column and treatment followed by the same letter are not different at the $\alpha = 0.05$ level. The absence of letters indicates that the F values for the main effects of tillage and rotation were not significant at the $\alpha=0.05$ level.

^c CC, continuous corn; CS, corn fb soybean; SC, soybean fb corn; COH, corn fb oat fb hay; OHC, oat fb hay fb corn; HCO, hay fb corn fb oat.

Table 4. Test statistic (*T*) from the multiresponse permutation procedure for paired comparisons to evaluate the main effects of tillage system and crop rotation on the weed seedbank community composition for 2002, 2003, and 2004.

Comparisons	2002	2003	2004
_		T	
CT ^a vs. MT	- 0.79 NS ^b	- 7.15 *	- 0.73 NS
CT vs. NT	- 5.06 *	- 12.69 *	- 4.91 *
MT vs. NT	- 2.55 NS	- 3.50 *	- 1.06 NS
CC vs. CS	- 1.49 NS	- 1.50 NS	- 0.64 NS
CC vs. SC	0.11 NS	- 0.93 NS	- 0.42 NS
CC vs. COH	- 8.58 *	- 4.63 *	- 3.55 NS
CC vs. OHC	- 5.32 *	- 4.85 *	- 2.32 NS
CC vs. HCO	- 4.36 *	- 4.82 *	- 4.01 NS
CS vs. SC	- 0.21 NS	- 0.84 NS	0.17 NS
CS vs. COH	- 9.38 *	- 5.78 *	- 6.32 *
CS vs. OHC	- 6.16 *	- 5.92 *	- 4.91 *
CS vs. HCO	- 6.49 *	- 5.69 *	- 7.17 *
SC vs. COH	- 9.29 *	- 4.02 *	- 6.96 *
SC vs. OHC	- 6.03 *	- 3.90 NS	- 5.57 *
SC vs. HCO	- 5.73 *	- 4.45 NS	- 7.59 *
COH vs. OHC	- 3.87 NS	0.47 NS	- 1.72 NS
COH vs. HCO	- 1.66 NS	- 0.78 NS	- 1.38 NS
OHC vs. HCO	0.12 NS	- 1.18 NS	- 2.39 NS

^a CT, conventional tillage; MT, minimum tillage; NT, no tillage; CC, continuous corn; CS, corn fb soybean; SC, soybean fb corn; COH, corn fb oat fb hay; OHC, oat fb hay fb corn; HCO, hay fb corn fb oat.

indicated that weed seedbanks in the CC, CS, and SC rotations did not differ significantly from each other. Because both crops received only glyphosate for weed control and have similar disturbance phenologies (e.g., spring tillage and planting and fall harvest), it is not unreasonable to expect that many of the same species would be supported by both systems. The weed seed communities in the CC, CS, and SC did differ significantly from those in the COH, OHC, and HCO. The continuous corn and the two-crop sequences provide a relatively predictable springtime environment where winter annual weeds have been killed by tillage or herbicide and summer annuals are managed with the use of a POST application of glyphosate. In contrast, the three-crop rotations require a disturbance (herbicide or tillage) during early spring in the oat year, midspring in the corn year, and late summer before the hay crop is planted. These disturbances provide for a varying habitat that may be suitable for infestation by species adapted to germinate and emerge at different times of the year. Despite the differences among the individual crop phases with respect to the type and timing of disturbances, there were no differences in community composition among the COH, OHC, and HCO seedbanks. Similar observations were made by Sosnoskie et al. (2006), who suggested seedbanks have been shaped by the cumulative effects of production practices and are buffered, to some extent, against year-to-year variations.

Except for the CT and NT comparison in 2002, emerged weed community composition was not affected by tillage (Table 5). Results from MRPP analyses indicated that there were no differences in the composition and structure of the aboveground weed communities in the CC, CS, and SC plots (Table 5). The weed community present in plots planted in the oat phase of the corn—oat—hay rotation differed significantly from the communities in plots planted to either corn or soybean (Table 5). Weed communities in HCO did not differ from communities in the CC, CS, and SC

Table 5. Test statistic (*T*) from the multiresponse permutation procedure for paired comparisons to evaluate the main effects of tillage and rotation on aboveground weed community composition for 2002, 2003, and 2004.

Comparisons	2002	2003	2004
_		T	
CT ^a vs. MT	$- 1.89 \text{ NS}^{\text{b}}$	– 0.53 NS	- 1.84 NS
CT vs. NT	- 5.31 *	- 1.01 NS	- 1.74 NS
MT vs. NT	– 2.69 NS	– 1.53 NS	- 2.04 NS
CC vs. CS	0.92 NS	0.66 NS	- 0.92 NS
CC vs. SC	0.65 NS	- 0.98 NS	- 2.77 NS
CC vs. COH	– 2.93 NS	- 4.54 *	- 4.15 *
CC vs. OHC	- 8.70 *	- 6.91 *	- 5.60 *
CC vs. HCO	- 4.32 NS	- 3.78 NS	- 2.06 NS
CS vs. SC	0.69 NS	- 0.99 NS	- 1.94 NS
CS vs. COH	- 3.05 NS	- 4.96 *	– 2.99 NS
CS vs. OHC	- 9.09 *	- 6.19 *	- 6.08 *
CS vs. HCO	- 3.99 NS	- 3.15 NS	- 1.56 NS
SC vs. COH	- 1.85 NS	- 5.12 *	- 5.40 *
SC vs. OHC	- 7.91 *	- 6.27 *	- 8.96 *
SC vs. HCO	- 2.76 NS	- 3.23 NS	- 3.34 NS
COH vs. OHC	- 4.19 *	- 5.64 *	- 6.01 *
COH vs. HCO	- 3.85 NS	- 3.13 NS	0.14 NS
OHC vs. HCO	- 4 . 87 *	0.77 NS	– 2.06 NS

^a CT, conventional tillage; MT, minimum tillage; NT, no tillage; CC, continuous corn; CS, corn fb soybean; SC, soybean fb corn; COH, corn fb oat fb hay; OHC, oat fb hay fb corn; HCO, hay fb corn fb oat.

treatments, whereas communities in COH did ($P \le 0.003$; Table 5). Except for 2002, the aboveground weed communities in the oat phase of the three-crop rotation differed from the corn phase but not the hay; the hay and the corn communities in the corn—oat—hay rotation did not differ from each other any year. Although the weed seedbanks for each phase of the corn—oat—hay rotation are indistinguishable from one another, MRPP analyses suggest that immediate disturbances are likely affecting the structure of the aboveground weed community.

Indicator Species Analysis. Indicator species were identified for the seedbank and emerged components of the weed community for the various tillage systems (Table 6) and crop rotations (Table 7). The number of significant indicator species in both the seedbank and the emerged weed communities was generally higher for NT (two to eight species) than for the other tillage systems (zero to three species). Except for 2002, the number of indicator species of the NT system was greater for the seedbank than for the emerged weed communities. Hairy bittercress (47 to 57% of perfect indication), annual fleabane [Erigeron annuus (L.) Pers.; 28 to 69%], foxtails (Setaria spp.; 49 to 64%), sowthistles (Sonchus spp.; 32 to 40%), speedwells (Veronica spp.; 50 to 54%), redroot pigweed (43 to 62%), common lambsquarters (65 to 81%), Pennsylvania smartweed (Polygonum pensylvanicum L.; 25 to 60%) and yellow woodsorrel (57 to 73%) were strongly associated with the NT seedbank and/or aboveground weed communities for two to three years. Dandelion was an indicator species for the emerged weed community in NT in 2002 (76%) and the MT seedbank in 2003 (53%). Annual bluegrass (Poa annua L.; 48 to 60%) and common chickweed [Stellaria media (L.) Vill.; 44 to 73%] were indicative of the MT system for 2003 (seedbank and emergent communities) and 2004 (seedbank community); common chickweed (53 to 71%) was also a significant

^b An asterisk indicates Bonferroni-corrected P values less than or equal to 0.015 and 0.003 for tillage and rotation, respectively. NS indicates that the treatments did not differ with respect to community composition.

^b An asterisk indicates Bonferroni-corrected P values less than or equal to 0.015 and 0.003 for tillage and rotation, respectively. NS indicates that the treatments did not differ with respect to community composition.

Table 6. Bayer codes (or genera names) of indicator species and percent of perfect indication for the springtime weed seedbank and emerged weed communities for tillage in 2002, 2003, and 2004.

		Seedbank		En	nerged we	eds
	CT ^a	MT	NT	СТ	MT	NT
			9	ó		
2002						
CARHI ^b	17	1	57*°	0	1	52*
CIRAR	_	_	_	0	0	53*
CYPES	41*	19	11	_	_	_
ERIAN	-	_	_	0	0	28*
LAMPU	1	6	42*	_	_	_
OXAST	13	24	57*	_	_	
POLAV	_	_	_	0	0	28*
POLPY	9	10	60*	_	_	-
Setaria spp.	_	_	_	2	14	49*
Sonchus spp.	_	_	_	0	3	40*
STEME	_	_	_	3	53*	3
TAROF	_	_	_	9	13	76*
Veronica spp.	_	_	_	2	1	54*
2003						
AMARE	9	14	43*	_	_	_
CARHI	2	27	52*	6	11	47*
CHEAL	13	21	65*	_	_	_
ERIAN	6	0	69*	_	_	_
OXAST	6	19	60*	_	_	_
PANDI	_	_	_	56*	19	12
POAAN	4	49*	0	25	60*	0
SENVU	_	_	_	3	3	31*
Setaria spp.	1	1	49*	4	13	64*
Sonchus spp.	0	4	32*	_	_	_
STEME	2	56*	5	15	71*	4
TAROF	5	53*	9	_	_	_
Veronica spp.	7	31	50*	_	_	_
2004						
AMARE	3	14	62*	_	_	_
CARHI	1	28	49*	_	_	_
CERVU	_	_	_	1	0	23*
CHEAL	4	7	81*	41*	37	2
Digitaria spp.	_	_	_	15	52*	16
ERIAN	1	3	28*	_	_	_
OXAST	4	11	73*	_	_	_
POAAN	4	48*	1	_	_	_
POLPY	2	1	25*	_	_	_
Setaria spp.	_	_	_	_	_	_
SOLPT	6	1	45*	_	_	_
Sonchus spp.	0	4	35*	_	_	_
STEME	0	44*	0	17	73*	0
Trifolium spp.	_	_	_	0	0	22*

^a CT, conventional tillage; MT, minimum tillage; NT, no tillage.

indicator of the emerged weed community in MT in 2002 and 2004. Yellow nutsedge (*Cyperus esculentus* L.; 41%) and fall panicum (56%) were indicators of the 2002 CT seedbank and 2003 CT emerged weed communities, respectively. Common lambsquarters was an indicator of both the NT seedbank (81%) and CT emerged weed (41%) communities in 2004. Of the 72 weed species observed throughout the course of the study, 21 (32%) functioned as an indicator species for at least one of the three tillage systems.

The number of significant (P ≤ 0.05) indicator species was generally greater in COH (1 to 10 species) and OHC (2 to 10) as compared to HCO (one to four), CC (zero to one), and CS and SC (zero to two; Table 7). Common lambsquarters was the only species that was strongly associated with CC (34 to 51% of perfect indication), although, in 2004, it was a significant indicator of the OHC (30%) emerged weed community. Annual bluegrass (32 to 81%) and common purslane (Portulaca oleracea L.; 36 to 55%) were the only indicators of the CS or SC seedbank and aboveground weed communities. Eighteen species, including hairy bittercress, crabgrasses, yellow woodsorrel, and foxtails, were classified as indicators of the three-crop rotation system (seedbank and/or emerged weed communities) for 2 of 3 yr. Twenty-nine of the 72 weed species (40%) identified over the course of the study were classified as an indicator species for one at least one of the crop rotation systems.

Some of the species classified as significant indicators of the tillage and rotation systems from 2002 to 2004 were also important constituents of the same systems from 1997 to 1999 (Cardina et al. 2002). Results from supplementary indicator species analyses performed on the 1997, 1998, and 1999 seedbank data were similar to those from the current study (data not shown). Annual bluegrass and common chickweed were significant indicators of the MT system for 2002, 2003, and 2004. Results showed that annual bluegrass was also a significant indicator of the MT seedbank for 1997, 1998, and 1999. Common chickweed was an indicator of MT in 1998, only. Yellow woodsorrel and foxtails were regular indicators of the NT seedbank for 1997, 1998, and 1999. Hairy bittercress, Pennsylvania smartweed, Lamium spp., and speedwells were indicators of NT for at least 1 yr from 1997 to 1999. These species were also indicative of the NT system in the current study. Fall panicum, which was a significant indicator of the NT seedbank from 1997 to 1999, was classified as an indicator of the aboveground weed community in CT in 2003 and 2004. As for the rotation systems, common lambsquarters was an indicator of the continuous corn system both before and after the switch to GTCs. The three-crop rotation from 1997 to 1999 was characterized by yellow woodsorrel, shepherd's-purse [Capsella bursa-pastoris (L.) Medicus], Pennsylvania smartweed, broadleaf plantain (Plantago major L.), witchgrass, sowthistles, crabgrasses, foxtails, speedwells, and clovers (Trifolium spp.), same as for 2002 to 2004.

Zanin et al. (1997) classified weed communities according to life form, periodicity types, dispersal types, and seed longevity with the aim of linking disturbance regimes with specific biological attributes. They reported a predominance of herbaceous perennials and woody shrubs with reduced tillage. Similarly, Kleyer (1999) studied the distribution of plant biological characteristics along a disturbance gradient in an agricultural landscape and noted that perennials were favored in areas where disturbance was minimal. Significant components of the NT and MT systems included two perennials, dandelion and Canada thistle [Cirsium arvense (L.) Scop.], along with yellow woodsorrel and common chickweed (both annual species that can become perennialized). Previous studies have found an association between NT systems and dandelion and Canada thistle (Légère and Samson 1999; Thomas et al. 2004). Annual grasses and wind-disseminated species are also predicted to increase when tillage intensity decreases (Streit et al. 2003). In our study, annual fleabane

b CARHI, Cardamine hirsuta L.; CIRAR, Cirsium arvense (L.) Scop.; CYPES, Cyperus esculentus L.; ERIAN, Erigeron annuus L. Pers.; LAMPU, Lamium purpureum L.; OXAST, Oxalis stricta L.; POLAV, Polygonum aviculare L.; POLPY, Polygonum pensylvanicum L.; STEME, Stellaria media (L.) Vill.; TAROF, Taraxacum officinale Weber in Wiggers; AMARE, Amaranthus retroflexus L.; CHEAL, Chenopodium album L.; PANDI, Panicum dichotomiflorum Michx.; POAAN, Poa annua L.; SENVU, Senecio vulgaris L.; CERVU, Cerastium vulgatum L.; SOLPT, Solanum ptycanthum Dun.

^c An asterisk indicates a significant maximum indicator value as determined with the use of a Monte Carlo test. A dash indicates that the species was an indicator of any treatment.

Table 7. Bayer codes (or genera names) of indicator species and percent of perfect indication for the springtime weed seedbank and emerged weed communities for rotation in 2002, 2003, and 2004.

		Seedbank					Emerged weeds					
	CCª	CS	SC	СОН	OHC	HCO	CC	CS	SC	СОН	OHC	HCC
2002							%					
											20*6	
AGRRE ^b	_	_	_	_	-	_	0	0	0	1	29*c	0
CAPBP	0	0	1	25	29*	23	_	-	_	- 0./*	_	_
CARHI	_	_	_	_	_	_	0	1	0	34*	6	1
CHEAL	_	_	_	_	_	_	34*	28	14	13	0	0
CYPES	_	_	_	_	_	_	0	0	1	1	0	27*
Digitaria spp.	1	8	1	49*	16	12	2	7	8	75*	3	0
LOBIN	3	0	1	63*	3	3	_	_	_	_	_	_
OXAST	2	1	2	47*	19	28	1	0	0	46*	38	4
PANDI	12	6	5	40*	1	19	31	3	1	45*	0	1
PLAMA	0	0	0	38*	20	22	0	1	0	51*	1	14
POAAN	_	_	_	_	_	_	0	64*	2	0	1	1
POLCO	_	_	_	_	_	_	0	0	0	70*	0	1
POLPY	_	_	_	_	_	_	0	0	0	32*	0	1
POROL	1	47*	3	0	1	2	2	55*	13	5	0	0
Rumex spp.	_	_	_	_	_	_	0	0	0	3	0	32*
Setaria spp.	5	2	3	65*	10	7	2	2	3	60*	3	0
SOLPT	3	8	12	1	29*	5	3	14	3	29*	0	0
Sonchus spp.	5	0	4	52*	1	3	4	0	1	4	0	44*
TAROF	5	0	4	52*	1	3	12	11	17	48*	12	10
Veronica spp.	1	3	2	22	31	35*	0	1	2	7	36*	3
003												
CAPBP	0	0	1	40	13	35	2	0	0	94*	0	1
CARHI	6	2	8	15	39*	7	2	3	2	11	50*	4
							48*					
CHEAL	51*	13	16	13	3	2		24	16	12	0	0
CYPES	_	_	-	_	-	-	0	0	0	44*	0	0
Digitaria spp.	1	2	1	6	11	65*	_	_	_	_	_	_
Festuca spp.	_	_	_	_	_	_	0	0	0	44*	0	0
LAMPU	_	_	_	_	_	_	0	0	0	3	5	42*
OXAST	1	1	1	40*	34	21	1	0	0	50*	31	14
PANCA	1	3	2	17	7	46*	2	15	3	41*	2	3
PANDI							12	4	4	45*	23	0
PLAMA	1	0	1	26	45*	17	0	0	0	72*	0	3
POAAN	2	2	81*	0	0	0	_	_	_	_	_	_
POLPY	0	0	0	43*	4	0	0	0	0	97*	0	0
POROL	_	_	_	_	_	_	6	23	36*	0	0	0
Setaria spp.	4	2	4	1	31*	0	_	_	_	_	_	_
Sonchus spp.	_	_	_	_	_	_	2	0	3	34*	0	5
TAROF	13	3	3	12	46*	0	_	_	_	_	_	_
THLAR	0	0	0	44*	1	1	0	0	0	65*	0	0
Trifolium spp.	_	_	_	_	_	_	1	1	0	2	58*	4
	_	_	_	_	_	_	1	1	U	2	76	4
004												
ABUTH	_	_	_	_	_	_	0	0	44*	0	0	0
CARHI	6	12	3	3	8	33*	_	_	_	_	_	_
CHEAL	_	_	_	_	_	_	25	8	3	2	30*	10
Digitaria spp.	8	2	2	38*	9	37	_	_	_	_	_	-
LAMPU	4	3	5	7	5	40*	_	_	_	_	_	_
MOLVE	0	5	34*	0					_		_	_
					0	0	_	_	_	_	- 22*	_
MUHFR	_	-	- 2	1.6	- 40*	26	0	0	0	0	33* 7.(*	0
OXAST	1	2	2	14	48*	26	0	0	0	4	76*	16
PANDI	11	3	1	9	24	44*	_	-	_	-	_	_
PLAMA	1	0	0	43*	33	14	0	1	0	12	44*	16
POAAN	3	32*	7	0	0	11	_	_	_	_	_	_
POLCO	_	_	_	_	_	_	2	0	0	0	28*	8
POLPY	0	0	0	0	29*	20	1	3	0	1	73*	4
POLAV	_	_	_	_	_	_	0	1	0	1	1	46*
POROL	_	_	_	_	_	_	1	38*	6	0	0	1
Rumex spp.	_	_	_	_	_	_	0	0	0	1	29*	0
Setaria spp.	3	1	2	5	10	48*	8	16	2	0	12	35*
SOLPT	_	_	_	_	_	_	0	3	0	2	52*	0
Sonchus spp.	0	1	2	5	25*	2	1	0	0	2	28*	2
TAROF												
	_	_	_	_	22*	_	_	_	_	_	- / ₄ / ₄ *	_
THLAR Trifolium spp.	0	0	0	0	33*	0	0	0	0	0	44*	0
I ritolium spp.	_	_	_	_	_	_	0	0	0	40*	0	17

^a CC, continuous corn; CS, corn fb soybean; SC, soybean fb corn; COH, corn fb oat fb hay; OHC, oat fb hay fb corn; HCO, hay fb corn fb oat.

^b AGRRE, Elymus repens (L.) Gould; CAPBP, Capsella bursa-pastoris (L.) Medicus; CARHI, Cardamine hirsuta L.; CHEAL, Chenopodium album L.; CYPES, Cyperus esculentus L.; LOBIN, Lobelia inflata L.; OXAST, Oxalis stricta L.; PANDI, Panicum dichotomiflorum Michx.; PLAMA, Plantago major L.; POAAN, Poa annua L.; POLCO, Polygonum convolvulus L.; POLPY, Polygonum pensylvanicum L.; POROL, Portulaca oleracea L.; SOLPT, Solanum ptycanthum Dun.; TAROF, Taraxacum

officinale Weber in Wiggers; LAMPU, Lamium purpureum L.; PANCA, Panicum capillare L.; THLAR, Thlaspi arvense L.; ABUTH, Abutilon theophrasti Medicus; MOLVE, Mollugo verticillata L.; MUHFR, Muhlenbergia frondosa (Poir.) Fern.; POLAV, Polygonum aviculare L.

^c An asterisk indicates a significant maximum indicator value as determined with the use of a Monte Carlo test. A dash indicates that the species was an indicator of any treatment.

and sowthistles, which are wind disseminated, were important constituents of the NT system. Annual bluegrass and foxtails were also consistently associated with reduced tillage.

Although annual broadleaves are expected to dominate under conventional tillage systems, we did not see any evidence for this in our study (Kleyer 1999; Streit et al. 2003; Tuesca et al. 2001). In fact, all of the annual broadleaved weeds, except for common lambsquarters in 2004, identified as indicator species were typical of the NT system. Regarding rotation, the most diverse system (corn, oats, and hay in rotation) was characterized by weed species that vary with respect to taxonomy, morphology, and phenology. For example, yellow woodsorrel and broadleaf plantain are spring/summer germinating perennials; crabgrasses, panicums, and foxtails are annual summer grasses; and shepherd's-purse and hairy bittercress are winter annuals. Understanding how agricultural practices have influenced the composition of weed communities should allow us to predict future problems in weed management, and may enable us to selectively favor certain, and possibly useful, weed communities over others (Anderson et al. 1998; Bàrberi and Lo Cascio 2001; Liebman 2001; Menalled et al. 2001; Tørresen and Skuterud 2002; Zanin et al. 1997). However, to accomplish this, more than just simple associations between basic life history traits and agronomic practices are required. According to Légère and Samson (1999) and Thomas et al. (2004), classification strategies based on more complex and quantitative biological aspects such as seed size, dormancy, dispersal and longevity, herbicide tolerance, water-use efficiency, and photosynthetic rate, are required to describe, adequately, species associations with agricultural systems.

Puricelli and Tuesca (2005) reported that the density and diversity of early-emerging broadleaved and grassy annuals decreased in response to regular glyphosate applications in systems planted to GTCs for up to 6 yr. Between 2002 and 2004, weed seedbank species richness in the current study decreased in 38 of 54 individual plots by an average of six species per plot, although it is impossible to say if this trend will continue with time (data not shown). For the same period, weed seed density increased in 43 of 54 plots by an average of 3,600 seeds m $^{-2}$ (data not shown). Additional analyses will be required to determine which species are increasing in number and if the reductions in species richness represent permanent losses to the weed communities or correspond to some sort of cyclical fluctuation in species diversity. As it appears that there may be little change in the identity of the dominant and the indicator species between the 1997 to 1999 and 2002 to 2004 studies, the lost species are likely to be infrequent members of the seedbank, such as Virginia copperleaf (Acalypha virginica L.), nodding beggarticks (Bidens cernua L.), boneset (Eupatorium perfoliatum L.), and stinging nettles (Urtica dioica L.).

The Triplett–Van Doren No-Tillage Experimental Plots have been actively maintained with the use of the most current weed control technologies available since 1962 (Cardina et al. 2002; Sosnoskie et al. 2006). In 1999, the plots transitioned away from standard soil-applied and postemergence herbi-

cides toward a weed management program that relied solely on glyphosate during the corn and soybean phases. The trends observed in weed seed and emerged plant density, diversity, and community composition after the adoption of glyphosate-tolerant corn and soybeans were also observed when soil-applied herbicides were the primary components of the weed management program in the study. Furthermore, many of the species classified as significant indicators of each tillage and rotation treatment from 2002 to 2004 were also important constituents of the same systems from 1997 to 1999 (Cardina et al. 2002). Herbicides play a role in shaping weed communities; however, in this study, the transition to GTCs, and the switch to a POST-applied glyphosate weed management protocol did not appear to significantly alter the weed seedbank communities in the short term (4 to 6 yr).

Sources of Materials

- ¹ Potting media ProMix BX, Premier Horticulture, Quakertown, PA 18951.
- ² SAS, version 9.0, Statistical Analysis System, Campus Drive, Cary, NC 27513.
- ³ PC-ORD Multivariate Analysis of Ecological Data, Version 3.01, MjM Software Design, P.O. Box 129, Gleneden Beach, OR 97388.

Acknowledgments

We thank Lynn Ault, farm manager for managing the field plots. The assistance of Bert Bishop and Larry Madden with the statistical analyses is gratefully acknowledged. Salaries and research support were provided by state and federal funds appropriated to the Ohio Agriculture Research and Development Center, The Ohio State University.

Literature Cited

Anderson, R. L., D. L. Tanaka, A. L. Black, and E. E. Schweizer. 1998. Weed community and species response to crop rotation, tillage and nitrogen fertility. Weed Technol. 12:531–536.

Bàrberi, P., A. Cozzani, M. Macchia, and E. Bonari. 1998. Size and composition of the weed seedbank under different management systems for continuous maize cropping. Weed Res. 38:319–334.

Bàrberi, P. and B. Lo Cascio. 2001. Long-term tillage and crop rotation effects on weed seedbank size and composition. Weed Res. 41:325–340.

Biondini, M. E., P. W. Mielke, Jr., and K. J. Berry. 1988. Data-dependent permutation techniques for the analysis of ecological data. Vegetatio 75:161–168.
 Blackburn, L. G. and C. Boutin. 2003. Subtle effects of herbicide use in the context of genetically modified crops: a case study with glyphosate (Round-

up®). Ecotoxicology 12:271–285.

Cardina, J., C. P. Herms, and D. J. Doohan. 2002. Crop rotation and tillage system effects on weed seedbanks. Weed Sci. 50:448–460.

Cardina, J. and D. H. Sparrow. 1996. A comparison of methods to predict weed seedling populations from the soil seedbank. Weed Sci. 44:46–51.

Carter, M. R. and J. A. Ivany. 2006. Weed seedbank composition under three long-term tillage regimes on a fine sandy loam in Atlantic Canada. Soil Tillage Res. 90:29–38.

Cavers, P. B. and D. L. Benoit. 1989. Seedbanks in arable land. Pages 309–328 in M. A. Leck, V. T. Parker, and R. L. Simpson, eds. Ecology of Soil Seedbanks. New York: Academic.

- Culpepper, A. S., T. L. Grey, W. K. Vencill, J. M. Kichler, T. M. Webster, S. M. Brown, A. C. York, J. W. Davis, and W. H. Hanna. 2006. Glyphosateresistant Palmer amaranth (Amaranthus palmeri) confirmed in Georgia. Weed Sci. 54:620-626.
- Davis, A. S., K. A. Renner, and K. L. Gross. 2005. Weed seedbank and community shifts in a long-term cropping systems experiment. Weed Sci. 53:296-306.
- Dick, W. A. and D. M. Van Doren, Jr. 1985. Continuous tillage and rotation combinations effects on corn, soybean, and oat yields. Agron. J. 77:459-465.
- Dufrêne, M. and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67:345-366.
- Duke, S. O. 2005. Taking stock of herbicide-resistant crops ten years after introduction. Pest Manag. Sci. 61:211-218.
- Feldman, F. and C. Boyle. 1998. Weed-mediated stability of arbuscular mycorrhizal effectiveness in maize monocultures. J. Appl. Bot. 73:1-5.
- Feldman, S. R., C. Alzugaray, P. S. Torres, and P. Lewis. 1997. The effect of different tillage systems on the composition of the seedbank. Weed Res. 37:71-76.
- Freyssinet, G. 2003. Herbicide-resistant transgenic crops—a benefit for agriculture. Phytoparasitica 31:105-107.
- Kleyer, M. 1999. Distribution of plant functional types along gradients of disturbance intensity and resource supply in an agricultural landscape. J. Veg. Sci. 10:697-708.
- Kuiper, H. A., G. A. Kleter, and M. Y. Nordam. 2000. Risks of the release of transgenic herbicide-resistant plants with respect to humans, animals and the environment. Crop Prot. 19:773-778.
- Légère, A. and N. Samson. 1999. Relative influence of crop rotation, tillage and weed management on weed associations in spring barley cropping systems. Weed Sci. 47:112-122.
- Légère, A., F. C. Stevenson, and D. L. Benoit. 2005. Diversity and assembly of weed communities: contrasting responses across cropping systems. Weed Res. 45:303-315.
- Leroux, G. D., D. L. Benoit, and S. Banville. 1996. Effect of crop rotation on weed control, Bidens cernua and Erigeron canadensis populations, and carrot yields in organic soils. Crop Prot. 15:171-178.
- Liebman, M. 2001. Weed management: a need for ecological approaches. Pages 1-30 in M. Liebman, C. L. Mohler, and C. P. Staver, eds. Ecological Management of Agricultural Weeds. Cambridge, UK: Cambridge University
- Liebman, M. and E. Dyck. 1993. Crop rotation and intercropping strategies for weed management. Ecol. Appl. 3:92-122
- Lyon, D. J., A. J. Bussman, J. O. Evans, C. A. Mallory-Smith, and T. F. Peeper. 2002. Pest management implications of glyphosate-resistant wheat (Triticum aestivum) in the western United States. Weed Technol. 16:680-690.
- Martinez-Ghersa, M. A., C. A. Worster, and S. R. Radosevich. 2003. Concerns a weed scientist might have about herbicide-tolerant crops: a revisitation. Weed Technol. 17:202-210.

- McCune, B. and J. B. Grace. 2002. Analysis of Ecological Communities. Gleneden Beach, OR: MjM Software Design. 300 p.
- Menalled, F. D., K. L. Gross, and M. Hammond. 2001. Weed aboveground and seedbank community responses to agricultural management systems. Ecol. Appl. 11:1586-1601.
- Powles, S. B. and D. L. Shaner. 2001. Herbicide Resistance and World Grains. Boca Raton, FL: CRC. 328 p.
- Puricelli, E. and D. Tuesca. 2005. Weed density and diversity under glyphosateresistant crop sequences. Crop Prot. 24:533-542.
- Riches, C. R. and B. E. Valverde. 2002. Agricultural and biological diversity in Latin America: implications for development, testing, and commercialization of herbicide resistant crops. Weed Technol. 16:200-214.
- Sosnoskie, L. M., C. P. Herms, and J. Cardina. 2006. Weed seedbank community composition in a 35-yr-old tillage and rotation experiment. Weed Sci. 54:263-273.
- Streit, B., S. B. Rieger, P. Stamp, and W. Richner. 2003. Weed populations in winter wheat as affected by crop sequence, intensity of tillage and time of herbicide application in a cool and humid climate. Weed Res.
- Sturz, A. V., B. G. Matheson, W. Arsenault, J. Kimpinski, and B. R. Christie. 2001. Weeds as a source of plant growth promoting rhizobacteria in agricultural soils. Can. J. Microbiol. 47:1013-1024.
- Swift, M. J. and J. M. Anderson. 1993. Biodiversity and ecosystem function in agricultural systems. Pages 14-41 in E. D. Schultz and H. A. Mooney, eds. Biodiversity and Ecosystem Function. Berlin: Springer.
- Thomas, A. G., D. A. Derksen, R. E. Blackshaw, R. C. Van Acker, A. Légère, P. R. Watson, and G. C. Turnbull. 2004. A multistudy approach to understanding weed population shifts in medium- to long-term tillage systems. Weed Sci. 52:874-880.
- Tørresen, K. S. and R. Skuterud. 2002. Plant protection in spring cereal production with reduced tillage. IV. Changes in weed flora and weed seedbank. Crop Prot. 21:179-193.
- Tørresen, K. S., R. Skuterud, H. J. Tandsæther, and M. Breddesen Hagemo. 2003. Long-term experiments with reduced tillage in spring cereals. I. Effects on weed flora, weed seedbank and grain yield. Crop Prot. 22:185-200.
- Tuesca, D., E. Puricelli, and J. C. Papa. 2001. A long-term study of weed flora shifts in different tillage systems. Weed Res. 41:369-382.
- Zanin, G., S. Otto, L. Riello, and M. Borin. 1997. Ecological interpretation of weed flora dynamics under tillage systems. Agric. Ecosyst. Environ. 66:177-188.
- Zimmerman, G. M., H. Goetz, and P. W. Mielke, Jr. 1985. Use of an improved statistical method for group comparison to study effects of prairie fire. Ecol. 66:606-611.
- Zoschke, A. 1994. Toward reduced herbicide rates and adapted weed management. Weed Technol. 8:376-386.

Received September 8, 2008, and approved January 12, 2009.